

STUDIES IN AUSTRALIAN MECOPTERA.

No. ii. THE WING-VENATION OF *CHORISTA AUSTRALIS* Klug.BY R. J. TILLYARD, M.A., D.SC., F.L.S., F.E.S., LINNEAN
MACLEAY FELLOW OF THE SOCIETY IN ZOOLOGY.

(Plate xliii.; and four Text-figures).

In collecting the evidence required for my work upon the Panorpid Complex, it was found necessary to examine the pupal tracheation of examples of all the Orders there studied. The only Order in which this had not yet been done (for at least one example of the Order) was the Mecoptera; in which so little is known of the life-histories, that it appears that only two observers, Brauer in Austria and Miyaké in Japan, have ever succeeded in following up the complete life-history of any single species. Neither of these authors was seized with the importance of making a study of the pupal wing-tracheation, although it is evident that the opportunity was offered to both of them.* The work of both was carried out upon the genus *Panorpa*, which is abundant enough in the Northern Hemisphere, but does not occur in Australia.

It was therefore necessary for me to set about the discovery of the pupa of some Australian representative of the Order. The only species that is at all common round Sydney is *Harpobittacus tillyardi* Esb.-Pet. But this belongs to a family that is, in many ways, the most highly specialised of all the Mecoptera; whereas, for my purposes, it was clear that an archaic representative of the Order was to be preferred. I therefore decided to follow up the life-history of the rare *Chorista australis* Klug, of which I

* Brauer's work was done long before the Comstock-Needham Theory of Venation saw the light. Miyaké's work is of recent date, but its objective was not venational, and the pupal wings were not examined.

had obtained only about seven specimens in the course of as many years.

Last year, I had the good fortune to find this rare species fairly commonly, for the first time since I had begun collecting insects around Sydney (about fourteen years). More fortunately still, the area in which they occurred was a very restricted one, only about a quarter of a mile from my house at Hornsby. In this locality, I took, in the course of three weeks' collecting in April, 1917, nearly one hundred specimens of this species. Several of the females laid eggs, but unfortunately none of these were fertile. I therefore watched carefully to see where the females appeared to be ovipositing, and determined to select a small area where there would seem to be a probability of finding the larvæ in February and March of this year.

As nothing is known of the life-history of this species, I worked upon the supposition that its larva would behave much as that of *Panorpa*; *i.e.*, that it would become rapidly full-fed, and then burrow into the ground and remain there for the greater part of the year, only pupating a week or two before the emergence of the imago. This supposition proved to be fairly correct. Digging and sifting of the soil in which the larva was expected to occur was begun in February and continued into March. The details of this arduous but interesting work are best left to be given in a full account of the life-history, which I hope to publish later on. Meanwhile, it will be sufficient to say that, one day in March, freshly turned pupæ were obtained, and that these were at once made use of for the purposes of this paper.

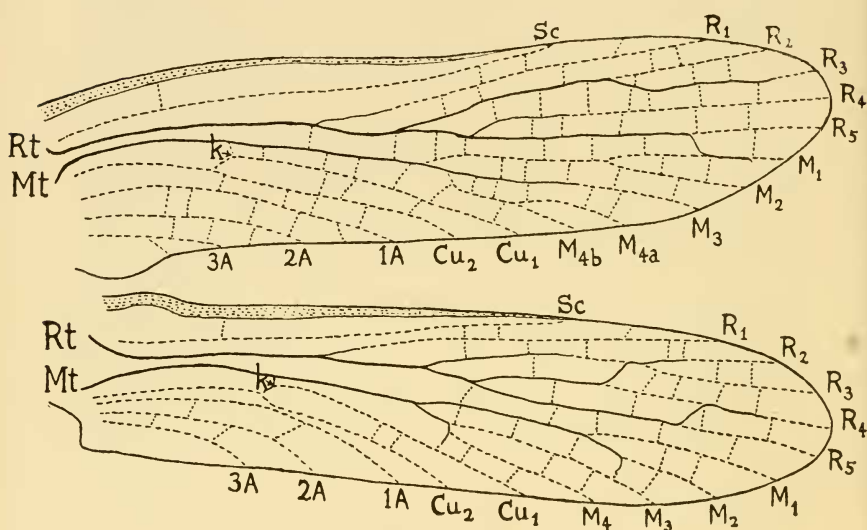
Owing to the shape of the pupa, and the direction of the wing-sheaths, which are laid more parallel to the abdomen than is usual in pupæ, it was not found practicable to use the method adopted previously in the case of *Chrysopa*. It was necessary to separate the wings from one another carefully, and to cut them off at their extreme bases with sharp scissors. As the wings are excessively delicate, this was not easy to do successfully. The photomicrographs obtained show how the delicate wings became creased near their middles, in the endeavour to separate the glued ex-

tremities; and also how, in the forewing, a portion of the fat-body, lodged in the extreme base of the wing, got carried over on to the wing when the cover-slip was let down upon it. Apart from this, the results obtained were quite satisfactory.

The Mecoptera are generally regarded as being an extremely archaic Order of Insects; and rightly so, for both in their general structure and in their Palaeontological record, the evidence tends to emphasise the fact that they are quite as old as any existing Holometabola, if not older. Within the Order, the genus *Chorista* is one of the most archaic types still extant, and shows close relationship to forms found in the Permian. I was therefore quite prepared, and indeed expectant, to find a very primitive and complete tracheational development in the pupal wings of this insect; and I was relying upon this to solve certain problems concerning the fusion of some of the main veins near the base of the wing, which cannot be determined with certainty from the imaginal venation. But the result obtained was quite different from what was expected; and, if there is any truth at all in the Comstock-Needham Theory of Wing-Venation, we must regard *Chorista* as a very highly specialised type in this one particular, if not in any other.

The facts of the case can be gathered very readily from a reference to the photomicrographs in Plate xliii., as well as the drawings in Text-fig. 1. *There are only two main trachea entering the wing-rudiment.* One of these belongs to the costo-radial group, and passes into the main stem of the radius. In the forewing, after giving off a very short and slender branch to R_1 , it passes on along the radial sector. At the forking of R_s into R_{2+3} and R_{4+5} , it follows the upper branch, giving off a fairly strong branch-trachea along the lower. Arriving at the forking of R_2 from R_3 , it bends weakly down into the latter, and does not reach the tip of the wing. The lower branch of this trachea passes along R_{4+5} into R_5 , giving off a short branch to R_4 , and finally ends up by bending down into R_{5b} . In the hindwing, there is only a minute vestige of the branch into R_1 . The main trachea passes on into R_s ; arriving at the fork of the sector, it gives off

only a weak branch into R_{2+3} , and passes on into R_{4+5} . Branches of about equal strength are given off to both R_4 and R_5 . The former passes up along a cross-vein into R_2 , while the latter performs a similar evolution nearer to the apex of the wing, ending up in R_4 .



Text-fig. 1.

Wings of a pupa of *Chorista australis* Klug, ♀, freshly-turned; ($\times 21$).

Semi-diagrammatic, the tracheation represented by continuous black lines, the imaginal venation by dotted lines; *k*, the point at which Cu_1 meets a short cross-vein from M , eventually fusing with M in the imaginal venation: *Mt*, median trachea; *Rt*, radial trachea. For rest of lettering, see p. 408.

The second main trachea of the wing is of smaller calibre, and belongs to the cubito-anal group. It enters the wing-rudiment along the media. In the forewing, it is quite unbranched, and passes finally into M_3 in an almost straight line. In the hindwing, it gives off short branches to the cubital fork and also to M_{3+4} , and its distal end passes into a cross-vein below M_2 .

A second pupa was examined and its wings photographed, but the negatives obtained were not very satisfactory. In this case,

the distal endings of some of the tracheæ were different from those recorded above; *e.g.*, the trachea in R_2 of the forewing passed down into R_4 viâ a cross-vein. The median trachea of the forewing also gave out a short branch to the cubital fork.

Only two pupæ were available for study. There can be little doubt that further minor variations would have been found had a longer series of pupæ been examined.

There is only one conclusion to be come to from this result. It is, that the Mecoptera, as exemplified by the archaic genus *Chorista*—and, therefore, presumably, by other existing genera—are highly specialised as an Order along the same lines that we find in the Hymenoptera, Trichoptera, and Diptera, viz., by the reduction of their wing-tracheation. The cause of this reduction is almost certainly the same in all four Orders, viz., that the tracheæ do not grow into the wing-rudiment until the latter has been fully formed, with the venational scheme completely laid down. In such a case, there is no longer any need for a tracheational scheme, to guide in the laying down of the venational scheme originally based upon it; the only necessity is to supply the wing with oxygen. Consequently, there will be a tendency to reduce the tracheal supply to the minimum necessary for this purpose; and, also, for the tracheæ to cease to follow their original paths, and to take instead the path of least resistance. Both these tendencies are well illustrated by the case here studied.

The same tendency, with many stages still preserved to us, has been noted already in the Order Plectoptera; an Order which, curiously enough, approaches most closely to the Holometabola, in that it possesses, in its sub-imaginal stage, what appears to have been Nature's first attempt to evolve a true resting-stage or pupa. The pupa of the archaic Mecoptera closely resembles the imago in everything except the form of its mouth-parts and the non-expansion of its wings. Thus it only differs from the sub-imago of the May-flies in being unable to fly, and in slightly less mobility of its free appendages. In the Order Plectoptera, there are a number of genera known in which the remaining wing-

tracheæ all come off from a single stem. This must be regarded as a higher specialisation than that found in the Mecoptera, or in any Holometabolous Order. For, in all of these, it would appear that *two* is the minimum number of wing-tracheæ yet reached in the course of evolution, *i.e.*, one from each of the main tracheal groups.

It is interesting to compare the courses of these two tracheæ in the four Holometabolous Orders which show reduction. Of the four, the only one which retains the media intact and separate from the base onwards is the Mecoptera. In this Order, the trachea belonging to the cubito-anal group passes into the media, which is as far forward as it could possibly get. This shows clearly that, in the ancestral form of the Mecoptera, the median trachea had already become attached to the cubito-anal group, as it has in most Orders of Insects. In the Hymenoptera, the media is suppressed in the imaginal venation, and only a bare vestige of its trachea is to be seen in a very ancient family, the *Siricidae*. The principal trachea of the cubito-anal group passes along the cubitus, and may or may not be accompanied by a separate anal trachea below it. In the highest forms, this latter becomes fused with the cubital trachea; so that the condition of two tracheæ only, in the wing-rudiment, is there fully reached. In the Trichoptera and Diptera, in which the media is fused basally with either the radius or the cubitus for a greater or less distance, the trachea of the cubito-anal group passes likewise along the cubitus.

From a study of this character only, then, it is clear that the Mecoptera present a more archaic stage than that seen in the Trichoptera and Diptera; and hence there is no evidence here *against* the presumption that both these Orders are derived from the older Mecoptera, as Handlirsch supposed. The Hymenoptera, on the other hand, cannot be derived from the Mecoptera, since they show a more archaic stage in the *Siricidae* and some other families (where more than two tracheæ are still present), even though they stand far in advance of the Mecoptera in having the media eliminated from their venational scheme.

Turning now to the Orders Lepidoptera and Planipennia, we see that both of these preserve the complete set of tracheæ in the pupal wing. In this character, then, they are both of them much more archaic than the Mecoptera and the other three Orders discussed above. It must be clear, therefore, on this character alone, that the Lepidoptera cannot be descended either from the Mecoptera, as Handlirsch supposed, or from the Trichoptera, as Meyrick would have it.

Let us now return to the question of the interpretation of the imaginal wing-venation in *Chorista*. The tracheation having failed us, what other evidence have we to go upon in working this out?

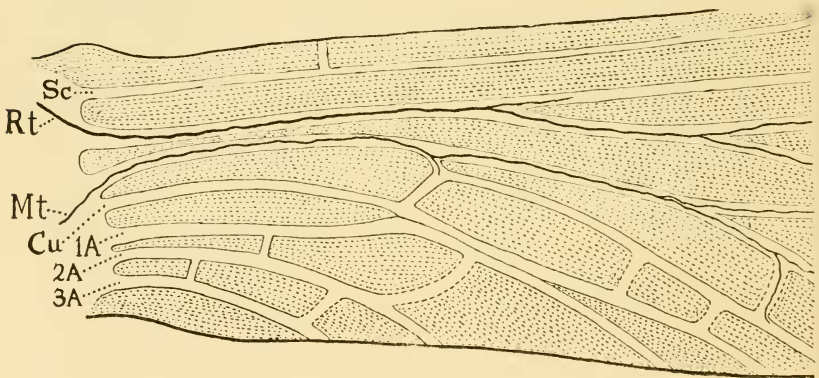
First of all, it may be stated that the main scheme of venation in *Chorista*, like that of the Trichoptera, is so primitive that there can be no hesitation in naming the veins, even though we cannot call upon the tracheæ as evidence. The subcosta, the radius, the radial sector with its dichotomous branches, and the anal veins can all be named without any misgivings. It is only the media and cubitus that offer a difficult problem. By referring to Text-fig. 1, it will be seen that the main stem of the media, in both fore- and hindwings, is continued straight on by a strongly convex vein right to the wing-border. All the rest of the media lies anteriorly to this. The media being properly a concave vein, it follows that there is at once a strong supposition that this straight prolongation of the media is really Cu_1 , and that the result has been brought about by a fusion of this latter vein, not far from its original at the cubital fork, with the main stem of the media.

If we examine the imaginal venation carefully, we shall see at once strong evidence in favour of this view. Picking up the base of the cubitus, which is a very weakly chitinised vein, and following it to the cubital fork (*cut'*), we see that the apparent cross-vein from this point to the media may very well be the basal portion of Cu_1 , arching up to unite with the media at the point *k*, and then leaving it again as the straight, strong, convex vein in question. If that be so, then Cu_2 in the forewing is the

vein that continues the line of the stem of Cu; while, in the hindwing, it must fuse with 1A for a short distance, and then separate from it again towards the wing-margin.

We must now ask for definite proof that this supposition is the correct one. That proof is forthcoming from two separate sources, viz., the pupal wing-venation, and the imaginal wing-venation. We may take these two separately.

(1) *Evidence from the pupal wing-venation*:—In the freshly turned pupa, less than one day old, the fusions of veins that take place in the imaginal venation are not completed, but only just beginning. (The photomicrographs in Plate xliii., are from a pupa at least three days old; those taken from a freshly turned pupa showed the separate veins much more distinctly, but unfortunately the negatives were partially spoiled through the use of stale developer, and are not good enough to reproduce).



Text-fig. 2.

Basal part of hindwing of same pupa as in Text-fig. 1, ($\times 43$), to show the radial (*Rt*), and median (*Mt*) tracheae, the approach of Cu_1 to *M*, and the partial fusion of Cu_2 with 1A.

Text-fig. 2 shows a camera-lucida drawing of the basal part of the hindwing of a freshly-turned pupa. In this, the separate veins Cu_2 and 1A can be clearly seen running alongside one another for some distance, and then diverging again towards the wing-margin. This fixes the position of *cuf* at the point already

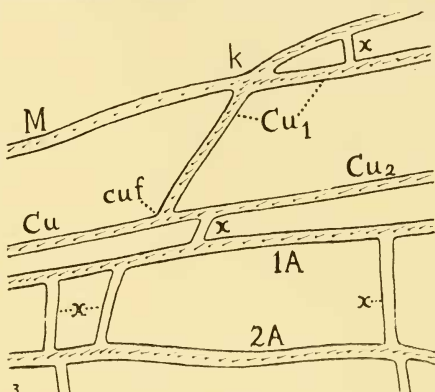
selected. The upwardly arching branch above *cuf* is seen to be connected with the media by a *short cross-vein* descending from the latter vein. In this pupal tracheation, then, the line of the median stem is not continued by Cu_1 , but by the true media; it is only a rearrangement of the positions of these parts in the imaginal venation that brings Cu_1 into the position of continuing the line of M.*

The case for the forewing is still simpler. Here there is no fusion of Cu_2 with 1A, and the parts of the cubitus can be seen to be quite separate from both M and 1A.

(2) *Evidence from the imaginal venation*:—The evidence that I propose to bring forward here is of quite a novel kind, and does not appear to have been used hitherto in any research upon wing-venation; yet it is of the utmost value.

In the wings of all Holometabolous Insects, two kinds of hairs or setæ are developed. These I have called *macrotrichia* and *microtrichia* respectively.† The former are, in most cases, restricted to the veins; the latter are spread indiscriminately,

and much more abundantly, over the whole of the wing. In the Mecoptera, the macrotrichia are found upon all the main veins and their branches, but *never upon the true cross-veins*. Hence



Text-fig. 3.

Part of the imaginal venation of the forewing of *Chorista australis* Klug, in the region of the cubital fork (*cuf*), to show distribution of the macrotrichia; ($\times 27$): *k*, the point at which Cu_1 has fused with M; *x*, cross-veins.

* Compare the somewhat analogous condition in the forewing of *Myrmecoptidae*, where Cu_{1a} captures M_2 close to its origin.

† "Mesozoic Insects of Queensland, No. 1." These Proceedings, 1917, xlii., Part 1, p. 195.

we have, here, a fine criterion for determining whether any supposed cross-vein is really such, or not.

Let us apply this to the basal portion of Cu_1 , which, arching up in the imaginal wing-venation to meet M , might well be mistaken for a cross-vein. From Text-fig.3, we see that all the cross-veins around it are destitute of macrotrichia. Not so this vein, however; for it is seen to carry a series of closely-set macrotrichia, which are continued along the rest of Cu_1 .

Further, it will be seen that the macrotrichia developed upon the media are less in number than those upon the cubitus, for any given length; those upon the cubitus being about twice as numerous. In this character also, the continuity of Cu_1 from *cu'* up to its fusion with M , and thence along the strong, convex vein already mentioned, is clearly indicated.

Putting the two sets of evidence together, there can be no doubt that the correct interpretation of the condition of the media and cubitus is that which is given in the Text-figures.

Description of the Wing-Venation. (Text-fig.4).

Having solved the above problem, we can now name all parts of the wing-venation without any doubt whatever. The result is shown in Text-fig.4. It will be seen that the wing-venational type is essentially similar to that of the Lepidoptera, Trichoptera, and Diptera, except for the fact that a considerable number of unspecialised cross-veins are developed as supports between the main veins. These cross-veins cannot be regarded as part of the original venation, since they do not carry macrotrichia, and are absent or very weakly developed in the oldest genera, both fossil and recent.

The *Subcosta* (*Sc*) is a straight vein terminating about halfway along the costal margin in the hindwing, somewhat beyond halfway in the forewing. In *Chorista*, it gives off only a single cross-vein in the costal space, near the base (occasionally, as in Text-fig.4, a second near its distal end). This is the homologue of the *humeral cross-vein* in Lepidoptera and Trichoptera, and is a true cross-vein, since it does not carry macrotrichia.

The *Radius (R)* is a strong convex vein branching at the radial fork (*r'*) into R_1 and R_s . The main stem, R_1 , reaches the wing-margin well before the apex. Around its distal end is formed the *pterostigma (pt)*, a hardened membranous area bounded by the costal margin above and the *pterostigmatic furrow (ptf)* beneath. Within this area are sometimes developed one or more *pterostigmatic veinlets*, which are also parts of the original venation, not cross-veins, but true branches of R_1 , since they carry macrotrichia. The *Radial Sector (Rs)* has the typical dichotomous branching seen in the Trichoptera, giving rise, in each wing, to four branches, R_2 , R_3 , R_4 , and R_5 respectively. The separation of R_2 from R_3 takes place far distad, under the pterostigma; that of R_4 from R_5 much further basad, not far from the first forking of R_s into R_{2+3} and R_{4+5} . All these branches are connected and strengthened by a number of cross-veins, whose position varies greatly in different individuals.

The *Media (M)* resembles the radial sector in the manner of its branching, as in Trichoptera; except that, in the forewing of *Chorista*, the most posterior of its four branches, M_4 , divides into two parts, M_{4a} and M_{4b} . The cross-vein connecting M_4 near its base with Cu_1 carries no macrotrichia, and must, therefore, be regarded as a true cross-vein, and not a branchlet from Cu_1 . Hence there is no evidence for the existence of the two branches of Cu_1 , which I have called Cu_{1a} and Cu_{1b} , and which are to be found in the most archaic Lepidoptera and in the Planipennia, but not in the Trichoptera.

The *Cubitus (Cu)* is two-branched, as in Trichoptera. The anterior branch, Cu_1 , arches upwards to connect with M , and then continues the line of M to the wing-margin as a strong, convex vein. The posterior branch, Cu_2 , in the forewing, simply continues the line of the main stem of Cu . In the hindwing, however, it fuses for some distance with $1A$, and then separates from it, and runs beneath Cu_1 to the wing-margin, at about half-way along the wing.

Three *Anal Veins* are developed in each wing. These remain

quite distinct throughout their courses, except for the partial fusion of 1A with Cu_2 already mentioned in the hindwing.

A number of cross-veins, irregularly placed and excessively variable in different individuals, are developed as supports between the branches of the media, the cubitus, and the anal veins.

It should be noted that, in the imaginal venation, the main stem of the media is fused with the radius for a short distance. In the pupal venation, these can be seen to be quite distinct.

SUMMARY.

(1) The tracheation of the pupal wing of *Chorista australis* is highly specialised by reduction, there being only two main tracheæ entering the wing. Of these, one belongs to the costo-radial group and passes into the radius; the other belongs to the cubito-anal group and passes into the media.

(2) In the freshly-turned pupa, the fusions of veins that are found in the imaginal venation are not accomplished, and hence it is possible to interpret the whole of the venation with certainty.

(3) Main veins and their branches, in the imaginal venation, carry macrotrichia; cross-veins do not. From this, it is demonstrable that an apparent cross-vein below M is in reality the basal portion of Cu_1 .

(4) The imaginal venation is specialised in having M fused basally with R for a short distance; in having Cu_1 continuing the line of the main stem of M, the short basal portion of Cu_1 resembling a cross-vein below M; and also in the partial fusion of Cu_2 with 1A in the hindwing.

(5) The rest of the venation is of a generalised type, closely resembling the typical Trichopterous plan, but with an extra branch to M_4 in the forewing. Cross-veins are fairly numerous, but variable in position and number in different individuals.

EXPLANATION OF PLATE XLIII.

Fig.1.—Wings of a pupa of *Chorista australis* Klug, ♀, three days old; ($\times 18$).

Fig.2.—Basal part of forewing of same; ($\times 43$). Note the Alar Trunk-Trachea at extreme base of wing, giving off the two wing-trachea.

Fig.3.—Basal part of hindwing of same; ($\times 32$).

(Photomicrographs of the freshly dissected wings in water).

EXPLANATION OF COMSTOCK-NEEDHAM VENATIONAL NOTATION, AS USED
IN THE TEXT-FIGURES.

1A, 2A, 3A, the three anal veins—C, costa—Cu, cubitus; Cu₁ its upper, and Cu₂ its lower branch—*caf*, cubital fork—*fr*, frenulum—M, media; M₁, M₂, M₃, M₄, its four branches, the last of which divides into M_{4a} and M_{4b} in the forewing—*mf*, median fork—*pt*, pterostigma—*ptf*, pterostigmatic furrow—R, radius, dividing into R₁, its main stem, and Rs, the radial sector; this latter has four branches, R₂, R₃, R₄, and R₅—*rf*, radial fork—*rf'*, fork of radial sector—Sc, subcosta.